

# Mammals of the San Pedro-Mezquital River Basin, Durango-Nayarit, Mexico

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**ABSTRACT:** The San Pedro–Mezquital River Basin is located in the southern Sierra Madre Occidental, at the Nearctic–Neotropical transition. The river traverses the Sierra through a canyon that reaches over 1000 m in depth. Based on examination of museum specimens, literature records, and our own collections, we documented the occurrence of 120 species (24.6% of the Mexican terrestrial mammals), 24 endemic to Mexico. Richness was comparable with other megadiverse areas of Mexico, and higher than any other Nearctic–Neotropical transition area, moreover species richness is likely to rise as survey continues. Contrary to expectation, distribution of mammals across the basin not only reflected the Nearctic–Neotropical divide, but a third fauna that is a mixture of tropical, temperate and desert species was identifiable at the canyon. Anthropogenic threats including damming of the river, uncontrolled cattle grazing, and pollution from domestic sources, call for effective management strategies to preserve one of the most biodiverse areas of Mexico.

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## Introduction

Mexico has one of the most diverse mammalian faunas in the world (525 species) surpassed only by Indonesia and Brazil (Ceballos *et al.* 2005). The great geographic and environmental complexity of Mexico and the mixture of Neotropical and Nearctic elements (Arita 1997; Ortega and Arita 1998; Morrone 2005) has produced a high variety of landscapes, climates, and vegetation types that result not only in a high species richness, but also in a large number of endemic taxa (Ceballos *et al.* 2005).

Despite past and recent efforts of survey and inventory, many areas of Mexico remain virtually unsampled, even for mammals, one of the best studied groups of animals. In particular, the Sierra Madre Occidental (SMO), most of which lies at the confluence of the Nearctic and Neotropical realm in northwestern Mexico, has been partially explored at best. Previous inventories that included the region (Baker and Greer 1962; Anderson 1972; Matson and Baker 1989) are partial and were focused on the most accessible regions, but many areas of this mountain range remain unexplored, particularly on the western versant, the most difficult to access. One of these areas is the San Pedro-Mezquital River Basin (SPMRB). This riverine system is located on the southern portion of the SMO, where the river cuts across the mountains from northeast to southwest, from its headwaters north of Durango City to its mouth at the Marismas Nacionales on the Pacific Plain of Nayarit (Figure 1). Along over 400 km, the San Pedro-Mezquital River traverses some of the most remote areas of the country. It is the Mexican river with the seventh largest water volume, as well as the last watercourse of the Pacific versant to remain undammed (WWF 2010) and the main source of fresh water for the Durango metropolitan area (ca. 460, 000

inhabitants, INEGI 2005). Additionally, it is one of the main providers of water for the Marismas Nacionales, the most widespread mangrove of the Mexican Pacific (20% of the Mexican mangroves), and an important sanctuary for birds and other vertebrates (CONANP 2007). Recently, the river has been identified as a potentially continuous corridor between the arid and semiarid vegetations of the Mexican Plateau and the tropical deciduous forest of the western slope of the SMO (González-Elizondo *et al.* 2007).

From its headwaters the river flows around the city of Durango, located on the western edge of the semiarid, temperate Mexican Plateau. South and east of the city a valley is formed with a difference of around 100 m between stream bed and ground level. As the river turns south near the village of Nombre de Dios and flows into the mountains, it excavates a canyon that can be from 800 to 1000 m deep in the central part of the mountain range. On the western side, about 80 km from the mouth, the terrain levels again and the river runs into an open valley on the coastal plain, nowadays covered with fragments of the original semideciduous forest, at an elevation ranging from 200 m to sea level at the Marismas Nacionales, where mangrove dominates. At the central portion of the basin, where the dominant vegetation is mixed conifer and oak forest on the highlands, within the canyon the microclimate allows for the development of semi-arid (on the eastern versant) and tropical vegetations (on the western flank; González-Elizondo et al. 2007).

Acknowledging the high biodiversity potential of this region, the Mexican Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO) has designated parts of the basin as Priority Terrestrial Regions (RTP 57, 58 and 61 Arriaga *et al.* 2000). Similarly,

the World Wildlife Fund (WWF) considers the basin of essential importance for water conservation (WWF 2010).

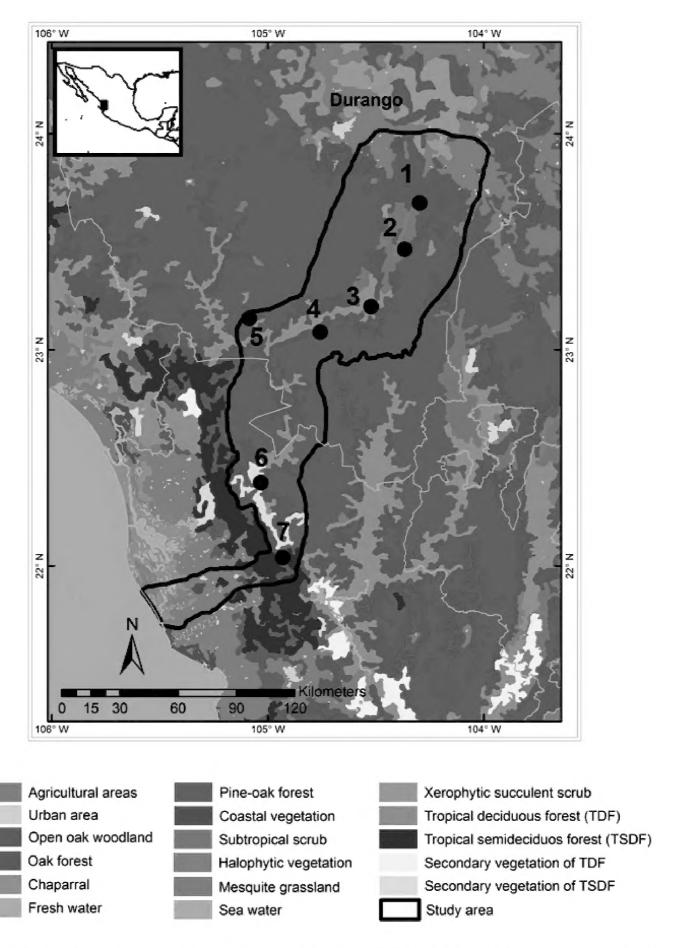
Notwithstanding the potential importance of the area for biodiversity and conservation, few published accounts exist on the fauna. In particular for mammals, most accounts concern the higher elevations of the basin (e.g., Baker and Greer 1962; Muñiz-Martínez 1997; Álvarez and Polaco 1984), but little is known about the lowlands (Crossin et al. 1973). The objective of this paper is to report the results of the first comprehensive attempt at inventorying the mammals of this potentially diverse region. This report is based on our own recent collections and observations, as well as on specimens previously collected by others and deposited in museums. We compared species richness and composition among the different vegetation types that occur in the basin. Based on species occurrences at each vegetation type, we explored the potential distributional patterns of species across the basin. Finally, we compared and contrasted our results with other, transitional and diverse regions of Mexico.

# **MATERIALS AND METHODS**

Study area

Although the SPMRB extends northwards as far as the municipality of Canatlán, in Durango, and as far southeast as Sombrerete, Zacatecas (WWF 2010), our collecting efforts focused on the portion spanning, from north to south, from the population of Nombre de Dios to the river mouth in Nayarit. From east to west the limits were set as 23.96° N, 103.97° W and 24.01° N, 104.54° W (Figure 1). For the purposes of this paper we modified the WWF polygon to include only the area of interest. The restricted polygon includes part of the municipalities of Durango, Nombre de Dios, Poanas, Vicente Guerrero, Súchil, Mezquital, and Pueblo Nuevo, in Durango state; and Huajicori, Acaponeta, Del Nayar, Rosamorada, Ruiz, Tuxpan and Santiago Ixcuintla, in the state of Nayarit.

The terrain of the basin is irregular, with a wide elevational gradient ranging from 0 to 3100 m above sea level. In general, vegetation in the area consisted originally of grasslands, scrublands and open woodland



**FIGURE 1.** Vegetation and limits of the San Pedro-Mezquital River Basin, modified from WWF (2010). Numbers represent intensive collection localities (see text). Agricultural areas and oak forests are depicted here as discrete categories, but they were further separated in eastern and western slope communities for analytical purposes.

("bosque bajo abierto", González-Elizondo *et al.* 2007) on the eastern versant; mixed pine-oak forests on the highlands; deciduous and semideciduous tropical forests on the lowlands; and palm groves and mangroves on the coast. On flat areas on both versants, original vegetation has been replaced by agriculture, and coffee is grown in the shade of semideciduous forests.

# Vegetation data

Vegetation categories follow those of INEGI (1998) digital map 1:1,000,000 (Figure 1) with some modification. We pooled the INEGI categories "pastizal-huizachal" and "mezquital" into a more general one, "mezquite grassland". "Bosque de pino" (pine forest) was included within "bosque de pino-encino" (pine-oak forest); "pastizal natural" (natural grassland), "pastizal inducido" (induced grassland) and "bosque bajo abierto" were included into "open oak woodland"; "selva baja espinosa" (tropical thorn shrub) and "selva baja caducifolia" (tropical deciduous forest) were pooled into tropical deciduous forest; and "manglar" (mangrove), "palmar" (palm forest), and "sabana" (savanna) were pooled into "coastal vegetation". Additionally, because plant species composition has different origins and affinities on each slope of the SMO, category "bosque de encino" (oak forest) was divided into "eastern oak forest" (occurring on the eastern, semiarid slope of the SMO), and "western oak forest" (occupying the western, tropical slope of the SMO). Similarly, all agricultural categories were divided into eastern slope agriculture (in semi arid regions) and western slope agriculture (tropical regions).

# Species data

We compiled a list of mammals of the SPMRB from specimens collected or observed by us, deposited in ours (CRD below), other scientific collections, or taken from literature records. Specimens are deposited at the Mammal Collection, Monte L. Bean Life Sciences Museum, Brigham Young University, Salt Lake City, USA (BYU); Museum of Michigan State University Mammal Collection, East Lansing, USA (MSU); Mammal Collection, Biodiversity Institute, University of Kansas, USA (KU); Texas Cooperative Wildlife Collection, Texas A&M University, College Station, USA (TCWC); Mammal Collection, CIIDIR-IPN Unidad Durango, Mexico (CRD), Mammal Collection, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, Mexico City (ENCB), Colección Nacional de Mamíferos, Instituto de Biología, Universidad Nacional Autónoma de Mexico, Mexico City (CNMA), and Colección de Mastozoología, Universidad Autónoma Metropolitana, Unidad Iztapalapa, Mexico City (UAMI). Only specimens from BYU were not examined by us, but records were taken from the BYU database. The arrangement of orders, families and subfamilies follows Wilson and Reeder (2005). Taxonomy and nomenclature of the order Soricomorpha follows Carraway (2007); for Stenodermatinae we follow Ceballos et al. (2005) and recognize Dermanura and Artibeus as genera, and A. intermedius J.A. Allen, 1897 as a valid species. For the genus *Dipodomys* we follow Fernández *et* al. (2012); for Natalus, Tejedor (2006) and López-Wilchis et al. (2012); for Sigmodon Peppers and Bradley (2000); for Neotoma Edwards et al. (2001); for Spermophilus

Helgen *et al.* (2009); for *Sturnira* Velazco and Patterson (2013); for *Thomomys* Hafner *et al.* (2011) and Mathis *et al.* (2013a). We also added to the species count *Thomomys sheldoni* Baird 1915, and *Thomomys atrovarius* (J.A. Allen, 1898), recently described from the area (Hafner *et al.* 2011; Mathis *et al.* 2013a). Literature records referring to species which taxonomic status may have changed in the area (*e.g., Peromyscus boylii* [Baird, 1855]) were not included. Protection status and endemism for each species are indicated following the IUCN red list (IUCN 2013) and current Mexican listings (NOM-059-ECOL-2010, SEMARNAT 2010). We did not include introduced or domestic species.

# Specimen collection

Between January 2009 and March 2011 sampling was conducted along the SPMRB in seven sites roughly 50 km distant from each other (Figure 1). With the exception of site 5, near San Francisco de Lajas, Durango, located at the Lajas River, a tributary, all sites were at the San Pedro-Mezquital River itself. We sampled each site for 10 nights, except site 4, which was sampled for 7 nights. At each site sampling was carried out at several locations, selected to try to cover as many vegetation associations present in the site as possible. Sampling focused on tropical or semiarid vegetation (below 1800 m above sea level). Rodents were captured using 400 Sherman traps baited with a mixture of oats and peanut butter, and were left at each sampling site for two nights to increase the probability of capture of "trap-shy" species. Bats were collected using ground-level mist nets placed along streams, ponds or in trails within forests, or taken by hand or with butterfly nets at roosts. Mist nets were left open for 5 hours after sunset. Large and medium-sized mammals were recorded in camera traps (5-14 depending on availability) set in animal trails, water holes, and potential refuges, or were captured in Tomahawk traps (5 traps). Cameras were left in place from one week to a month. We performed diurnal and nocturnal transects on roads and trails to search for tracks, footprints, osteological material, and to record direct observations. Sampling effort was comparable among sites for bats and rodents, but not for large and mediumsized mammals. Additional opportunistic collections took place on a number of localities within the basin. Specimens were prepared following conventional techniques in mammalogy, and were deposited in the Mammal Collection, CIIDIR-IPN Unidad Durango (SEMARNAT collection permit FAUT-0085 to CLG). Specimens collected by us and deposited at CRD were handled and processed following the guidelines of the American Society of Mammalogists (Sikes et al. 2011). Our field records were georeferenced using a GPS receiver. Coordinates for specimens from other collections or literature records were approximated using Google Earth ver. 5.1.3533.1731.

# Data analysis

Using the tool "Spatial Join" from ArcMap GIS, ver. 9.3 (ESRI Inc. 2008, Redlands CA, USA) we associated each mammal record to a vegetation type in the basin. From these data we created a matrix of presence-absence of species (rows) by vegetation type (columns). To examine patterns of species distributions, *i.e.*, how

similar are species in their distributions across the basin, we performed an R-mode cluster analysis (Ludwig and Reynolds 1988) using the species-by-vegetation matrix. Conversely, to explore patterns of species composition by vegetation type, *i.e.* how similar are vegetation types in their species composition, we ran a Q-mode analysis on the same data matrix. For both analyses we used the one-complement of the Jaccard index (Brower and Zar 1977; Ludwig and Reynolds 1988; Tuomisto 2010) as a measure of distance, and UPGMA (Sneath and Sokal 1973) as grouping algorithm. We performed the analysis using PAST ver. 2.07 (Hammer et al. 2001). Because volant and non-volant mammals, and small and large mammals use the landscape differently (Arita 1997; Rodríguez et al. 2003), the mammalian assemblage of the basin was broken into three groups that were analyzed separately: 1) Rodents (Rodentia) and shrews (Soricomorpha), 2) bats (Chiroptera), and 3) medium-sized and large mammals (Carnivora, Artiodactyla, Lagomorpha, Cingulata, and Didelphimorphia except *Tlacuatzin*, which was included in group 1). Species richness at the SPMRB was compared by order with that of the entire country, and with 12 intensively sampled megadiverse areas of Mexico (Table 1). For each site, species richness and number of endemic species was calculated and plotted using Microsoft Excel for Windows 2007.

#### RESULTS

Species richness

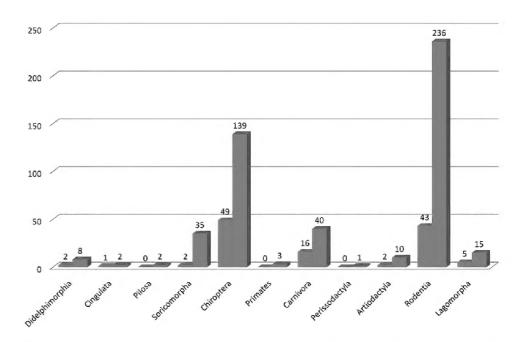
We recorded 120 species of mammals belonging to 8 orders, 23 families, and 71 genera (Table 2), which represent 24.6 % of the terrestrial mammalian fauna of Mexico (485 species, Ceballos et al. 2005). Chiroptera was the most species-rich order (49 species), followed by Rodentia (43 species), and Carnivora (16 species, Figure 2). Sixty-eight species had Nearctic affinities and 52 had Neotropical affinities. Eighteen (15.1%) are species of concern (7 rodents, 5 bats, 5 carnivores, and 1 shrew, Table 2), and 24 (20 %) were endemic to Mexico (17 rodents, 4 bats, 1 shrew, 1 opossum, and 1 rabbit, Table 2), which represent 14.9% of Mexican endemics (161, Ceballos et al. 2005). The proportion of species of the most speciesrich orders that occur in the basin does not mirror that of Mexico as a whole. Bats seem to be overrepresented (40.8% of the mammals in SPMRB, 28.2 % for Mexico),

as well as carnivores (13.3% vs. 8.2%), and lagomorphs (4.2% vs. 3.1%), whereas rodents (35.8% vs. 48.5%) and shrews (1.7% vs. 6.6%) seem underrepresented.

Patterns of species composition by vegetation type

At least one specimen was recorded in 14 of 16 vegetation types occurring in the basin (Figure 1). The highest species richness was recorded in pine-oak forest (62 species), followed by subtropical scrub ("matorral subtropical", 50 species), and tropical deciduous forest ("bosque tropical caducifolio" 46 species). Xerophytic succulent scrub ("matorral crasicaule") and coastal vegetation showed the lowest species richness (4 and 5 species, respectively), although the low richness found here is more likely the result of the relatively lower collection efforts in this area compared to the rest of the basin.

The cluster analysis grouped the 14 vegetation types into three clearly differentiated groups (Figure 3): 1) arid (xerophytic succulent scrub) and semiarid regions (chaparral and eastern oak forest) all from the eastern versant of the SMO, and common in the northern portion of the basin. Species composition is heterogeneous among these vegetation associations, eastern oak forest and chaparral shared only 20% of the species; and both groups together shared only 15% of species with xerophytic succulent scrub. This group includes mammal



**FIGURE 2.** Mammal species richness by order at the San Pedro-Mezquital River Basin (orange bars) and Mexico (green bars). Data for Mexico from Ceballos *et al.* (2005).

TABLE 1. Mexican megadiverse mammal communities used for comparison with SPMRB (Figure 7).

SOURCE
This study
Monteagudo-Sabaté and León-Paniagua (2002)
Monteagudo-Sabaté and León-Paniagua (2002)
Íñiguez-Dávalos and Santana-Castellón (2005)
León-Paniagua <i>et al.</i> (2004)
Martínez-Gallardo and Sánchez-Cordero (1997)
González-Christen (2008)
Espinoza-Medinilla et al. (1998)
Medellín (1994)
Monteagudo-Sabaté and León-Paniagua (2002)
Olguín-Monroy et al. (2008); García-García and Santos-Moreno (2008)
N. González-Ruiz (in litt.)
Monteagudo-Sabaté and León-Paniagua (2002)

species of Nearctic affinities, mostly vespertilionid bats and cricetid rodents. 2) Plant associations of the western slope of the SMO and coastal plains of Navarit (western oak forest, tropical semideciduous forest and secondary vegetation derived from it, western agriculture and coastal vegetation). This also is a heterogeneous group; no subgroup shared more than 36% of the species. This group included mainly Neotropical species. 3) Tropical deciduous forest and subtropical scrub, open oak woodland (an association typical of the eastern foothills of the SMO), eastern slope agriculture, pine-oak forests, and urban areas. Subtropical scrub and tropical deciduous forest shared 53% of the species; together, they shared 34% of the species with pine oak forest (Figure 3). Open oak woodland and eastern slope agriculture shared 37% of the species, and together they shared 25% with the other subgroup (Figure 3). This cluster includes both Nearctic and Neotropical associations, some occurring on the eastern and some on the western versant of the SMO, their common denominator is that all occur on the river valley.

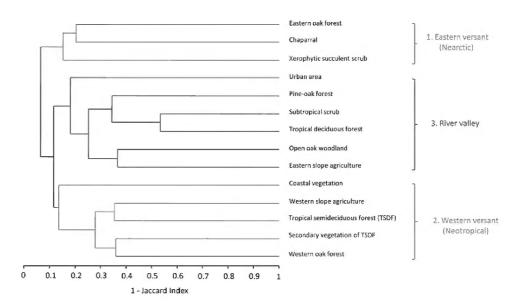
# Patterns of species distributions across the basin

In general the cluster analysis recovers the Nearctic-Neotropical divide for bats (Figure 4). Only two species, Lasiurus xanthinus (Thomas, 1897) and Glossophaga commissarisi Gardner, 1962, for which there is only one record, do not conform to this pattern. Further, within the Neotropical cluster a major subgroup is formed including species that occur only on the Pacific coastal plain, but not at the piedmont or highlands of the SMO. The Nearctic cluster also includes two major groups, bats that were captured at the highlands only, and bats with a more widespread distribution in dry tropics and semi-desert biomes. Exceptions to the pattern are Myotis yumanensis (H.A. Allen, 1864) and Myotis californicus (Audubon & Bachman, 1842), species of Nearctic affinities that occur along the river valley at least to San Blasito, Nayarit, less than 100 km from the coast (Site 6, Figure 1). Similarly, Artibeus hirsutus K. Andersen, 1906 and Dermanura azteca (K. Andersen, 1906), neotropical bats, clustered with nearctic species because they have been captured along the river valley as far inland as the town of Mezquital (A. hirsutus) or as high as 2500 m above seal level, in pine-oak forest (*D. azteca*, Figure 4).

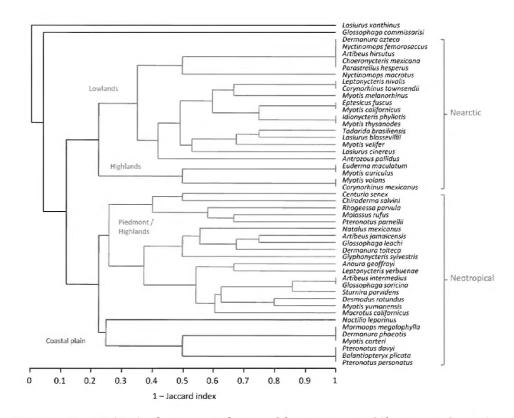
For rodents, shrews and the marsupial Tlacuatzin the ordination also clusters Nearctic and Neotropical species (Figure 5). For the Nearctic group four clusters are recognizable, one including species distributed in pineoak associations, one including species widely distributed on the Mexican Plateau, and one that also is distributed in pine-oak associations, but only in the highest portions of the SMO. Unlike bats, however, the fourth cluster includes species of both affinities that have in common to be distributed along the canyon, e.g., Liomys pictus (Thomas, 1893), Sigmodon arizonae Mearns, 1890, Baiomys taylori (Thomas, 1887), and Neotoma mexicana Baird, 1855, in a variety of vegetation associations and elevations. The remaining species (Perognathus flavus Baird, 1855, Dypodomys ornatus Merriam, 1894, Onychomys arenicola Mearns, 1896, and Xerospermophilus spilosoma [Bennett, 1833]), are of Nearctic affinities and occurred

at the tropical-desert transition, but only one record was available for each, thus no grouping was possible.

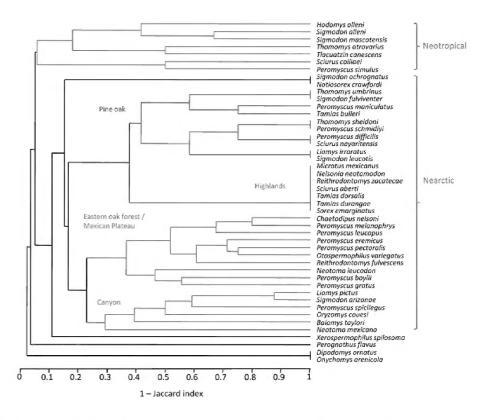
For mid-sized and large species, the Nearctic-Neotropical divide is not evident (Figure 6). Instead, four clusters exist that may represent species widely



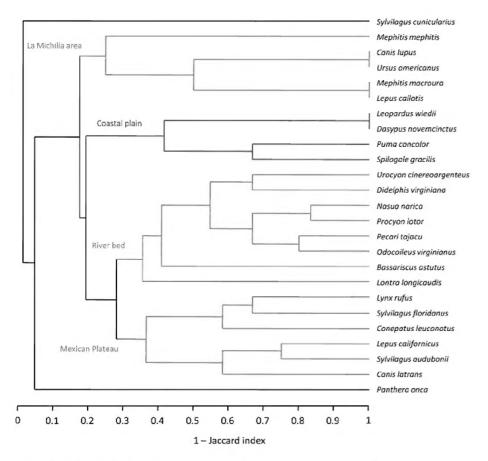
**FIGURE 3.** UPGMA cluster analysis of vegetation types at the San Pedro-Mezquital River Basin, based on similarity in mammal species composition.



**FIGURE 4.** UPGMA cluster analysis of bat species (Chiroptera) at San Pedro-Mezquital River Basin based on their habitat (vegetation type) similarity.



**FIGURE 5.** UPGMA cluster analysis of small non-volant mammals (Soricomorpha, Rodentia, *Tlacuatzin*) at San Pedro-Mezquital River Basin based on their habitat (vegetation type) similarity.

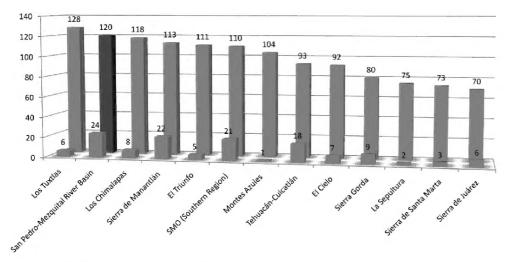


**FIGURE 6.** UPGMA cluster analysis of medium-sized and large mammals (Artiodactyla, Carnivora, Cingulata, Didelphimorphia, and Lagomorpha) at the San Pedro-Mezquital River Basin based on their habitat (vegetation type) similarity.

distributed in the Mexican Plateau, species that occur on the river bed, species that were captured in tropical lowlands, and species collected on the tropical versant. Nonetheless, because data available on these species are scant and focused either on the river bed (our sampling) or at and near La Michilía Reserve (Baker and Greer 1962; Álvarez and Polaco 1984), these clusters may actually be reflecting sampling biases, *i.e.* major efforts have been made at La Michilía and on the river bed.

## Comparisons with similar areas

Species richness at SPMRB (120 species) was lower than at Los Tuxtlas reserve (128), but comparable to that of other neotropical rainforest sites like Los Chimalapas (118) and El Triunfo (111) two of the most diverse areas in Mexico (Figure 7, Martínez-Gallardo and Sánchez-Cordero 1997; Espinoza-Medinilla *et al.* 1998; Olguín-Monroy *et al.* 2008), and transitional sites like Sierra de Manantlán (113) and Sierra Madre Oriental (110), at the Nearctic-Neotropical transition in central Mexico (León-Paniagua *et al.* 2004; Íñiguez-Dávalos and Santana-Castellón 2005). Other Nearctic-Neotropical transitions such as Tehuacán-Cuicatlán (93), El Cielo (92), Sierra Gorda (80), and Sierra de Juárez (70) had considerable lower species richness



**FIGURE 7.** Species richness (blue bars) and number of endemisms (red bars) at the San Pedro-Mezquital River Basin (grey bar) compared with other megadiverse, intensively sampled areas of Mexico (Table 2).

(González-Ruiz *in litt.*; Monteagudo-Sabaté and León-Paniagua 2002). The number of endemic species that occur at the SPMRB (24) is comparable only to Manantlán (22), Sierra Madre Oriental (21) and Tehuacán-Cuicatlán (18).

#### **DISCUSSION**

Mammals were recorded in 14 vegetation types within the basin (Table 2; Figures 1 and 3). It is noteworthy that when vegetation types are grouped by similarity in species composition, instead of two major clusters, as it would be expected (Nearctic and Neotropical), 3 were identifiable. Two of those groups indeed correspond to vegetation associations that occur on the Nearctic and Neotropical side of the SMO (groups 1 and 2, respectively, Figure 3), but a third group that included vegetation types from both regions was also evident. Nonetheless, when data are grouped by species that occur in the same vegetation type, the Nearctic–Neotropical division is recovered by the UPGMA for small mammals, both volant and non-volant (Figures 4 and 5).

On the other hand, the highest species richness of the basin was recorded in pine-oak forest, and not in tropical vegetation associations as it would be expected. There is a difference of at least 11 species between pine-oak communities (62 species) and the next most specious vegetation types, subtropical scrub (50 species) and tropical deciduous forest (46). The vegetation types with the highest species richness are those included in group 3 of Figure 3, and not those of the Neotropical group. Moreover, vegetation associations within group 3 share a higher proportion of species than those in the Nearctic or Neotropical clusters.

These observations can be explained by the particular physiographic (and therefore climatic and vegetational) complexity of the basin. Although for practical purposes we used the vegetation categories of INEGI (2010), in reality, and in particular in the area around the town of Mezquital (site 2 in Figure 1), where the river valley is wide (about 7 km), we observed that elements of xerophytic vegetations occur in tropical and subtropical associations, and vice versa. Also, on the central portion of the basin (where the river valley narrows down) the Sierra rises over 2400 m above sea level, whereas the river bed is 1000 m lower. In these areas, a strong vegetational gradient occurs, from pine to pine-oak, western oak, and tropical deciduous forest at the river bed. This transition occurs in short distances, and elements of any given association are mixed with elements of the one below and above it.

Thus, many mammal species that otherwise would be confined to one vegetation association, at the SPMRB can occur in more than one, probably tracking specific resources that are able to occur in more than one plant association along the elevational/vegetational gradient. As a result, some species were found in vegetation types and places where they usually do not occur, and the proportion of shared species increases in these areas. For instance, species of Neotropical affinities like the opossum *Tlacuatzin canescens* (J.A. Allen, 1893) or the moustached bat *Pteronotus parnellii* (Gray, 1843), which inhabit the tropical deciduous and semideciduous forests of the coastal plain, reach far north into the mountains following

**TABLE 2.** Mammals of the San Pedro-Mezquital River Basin. Conservation status (CO) according to NOM-ECOL-059-2010 (SEMARNAT 2010) and IUCN (2013) as follows: A = Threatened, Pr = Special protection, P = Endangered, VU = Vulnerable, EN = Endangered, E = Extinct. Column E = endemic of Mexico. Vegetation types as in Figure 1: UA = urban area, EA = agriculture eastern slope, XS = xerophytic succulent scrub, WD = open oak woodland, SS = subtropical scrub, CH = chaparral, EO = eastern oak forest, PO = pine-oak forest, TD = tropical deciduous forest WO = western oak forest, TS = tropical semi-deciduous forest, STS= secondary vegetation of tropical semi-deciduous forest, CV = coastal vegetation, WA = agriculture western slope.

								ION T							СО	E
	UA	EA	XS	WD	SS	СН	EO	PO	TD	wo	TS	STS	CV	WA		_
Order Didelphimorphia																
Family Didelphidae																
Subfamily Didelphinae																
Didelphis virginiana Kerr, 1792	X	X			X			X	X	X	X	X				
Tlacuatzin canescens (J.A. Allen, 1893)									X			X				X
Order Cingulata																
Family Dasypodidae																
Subfamily Dasypodinae																
Dasypus novemcinctus Linnaeus, 1758												X				
Order Lagomorpha																
Family Leporidae																
Lepus californicus Gray, 1837	X	X		X	X											
Lepus callotis Wagler, 1830				X				X								
Sylvilagus audubonii (Baird, 1858)	X			X	X											
Sylvilagus cunicularius (Waterhouse, 1848)											X					X
Sylvilagus floridanus (J.A. Allen, 1890)					X			X								
Order Soricomorpha																
Family Soricidae																
Subfamily Soricinae																
Notiosorex crawfordi (Coues, 1877)				X											Α	
Sorex emarginatus Jackson, 1825								X								X
Order Chiroptera																
Family Emballonuridae																
Subfamily Emballonurinae																
Balantiopteryx plicata Peters, 1867											X			X		
Family Phyllostomidae																
Subfamily Desmodontinae																
Desmodus rotundus (É. Geoffroy, 1810)					X				X		X	X				
Subfamily Glossophaginae																
Anoura geoffroyi Gray, 1838					X			X	X	X	X					
Choeronycteris mexicana Tschudi, 1844					X				X						Α	
Glossophaga commissarisi Gardner, 1962										X						
Glossophaga leachii Gray, 1844										X	X	X				
Glossophaga soricina (Pallas, 1766)					X				X	X	X	X		X		
Leptonycteris nivalis (de Saussure, 1860)					X			X							A/EN	
Leptonycteris yerbabuenae Martínez & Villa-R.	,			X	X			X	X		X				A/VU	
1940				Λ	Λ			Λ	Λ		Λ				11, 70	
Subfamily Phyllostominae																
Glyphonycteris sylvestris Thomas, 1896										X	X					
Macrotus californicus Baird, 1858					X			X	X	X		X				
Subfamily Stenodermatinae																
Artibeus hirsutus K. Andersen, 1906					X				X							X
Artibeus intermedius J.A. Allen, 1897					X				X	X	X	X		X		
Artibeus jamaicensis Leach, 1821										X	X	X		X		
Centurio senex Gray, 1842									X		X					
Chiroderma salvini Dobson, 1878									X							
Dermanura azteca (K. Andersen, 1906)					X				X							
Dermanura phaeotis Miller, 1902											X					
Dermanura tolteca (de Saussure, 1860)									X	X	X	X				
Sturnira parvidens Goldman, 1917					X			X	X	X	X	X		X		
Family Mormoopidae																
Mormoops megalophylla (Peters, 1864)											X					
Pteronotus davyi Gray, 1838											X			X		
Pteronotus parnellii (Gray, 1843)									X		X			X		
Pteronotus personatus (Wagner, 1843)											X			X		
Family Noctilionidae																
Noctilio leporinus (Linnaeus, 1758)														X		



 TABLE 2. Continued.

	VEGETATION TYPE												СО			
	UA	EA	XS	WD	SS	СН	EO	PO	TD	wo	TS	STS	CV	WA	CO	
Family Natalidae																
Natalus mexicanus Miller, 1902											X	X				
Family Molossidae																
Subfamily Molossinae																
Molossus rufus È. Geoffroy StHilaire, 1805									X					X		
Nyctinomops femorosaccus (Merriam, 1889)					X				X							
Nyctinomops macrotis (Gray, 1839)					X											
Tadarida brasiliensis (I. Geoffroy, 1824)	X				X			X	X							
Family Vespertilionidae																
Subfamily Vespertilioninae																
Eptesicus fuscus (Palisot de Beauvois, 1796)					X	X		X	X							
Lasiurus blossevillii (Lesson & Garnot, 1826)	X				X	Λ		X	Λ							
				v	X	v			v							
Lasiurus cinereus (Palisot de Beauvois, 1796)	X	v		X	Λ	X	v	X	X							
Lasiurus xanthinus (Thomas, 1897)		X					X		**			**		**		
Rhogeessa parvula H. Allen, 1866									X			X		X		
Parastrellus hesperus (H. Allen, 1864)					X				X							
Corynorhinus mexicanus G.M. Allen, 1916						X		X								
Corynorhinus townsendii (Cooper, 1837)					X			X								
Euderma maculatum (J.A. Allen, 1891)								X							Pr	
Idionycteris phyllotis (G.M. Allen, 1916)					X	X		X								
Subfamily Antrozoinae																
Antrozous pallidus (Le Conte, 1856)		X		X	X			X								
Subfamily Myotinae																
Myotis auriculus Baker & Stains, 1955								X								
Myotis californicus (Audubon & Bachman, 1842)					X	X		X	X							
Myotis carteri LaVal, 1973					Λ	Λ		Λ	Λ		X				Pr	
					v			v	X		Λ				ГІ	
Myotis melanorhinus (Merriam, 1886)					X	77		X	Χ							
Myotis thysanodes Miller, 1897					X	X		X								
Myotis velifer (J.A. Allen, 1890)	X	X			X			X								
Myotis volans (H. Allen, 1866)						X		X								
Myotis yumanensis (H. Allen, 1864)					X			X	X		X	X				
Order Carnivora																
Family Felidae																
Subfamily Felinae																
Leopardus wiedii (Schinz, 1821)												X			P	
Lynx rufus (Schreber, 1777)		X			X			X								
Puma concolor (Linnaeus, 1771)								X				X				
Subfamily Pantherinae																
Panthera onca (Linnaeus, 1758)										X					P	
										Λ					1	
Family Canidae	77	37		37	37		7.7	37								
Canis latrans Say, 1823	X	X		X	X		X	X							_	
Canis lupus Linnaeus, 1758								X							E	
Urocyon cinereoargenteus (Schreber, 1775)	X	X		X	X			X	X			X				
Family Ursidae																
Ursus americanus Pallas, 1780¹								X							P	
Family Mustelidae																
Subfamily Lutrinae																
Lontra longicaudis (Olfers, 1818)								X	X	X	X				Α	
Family Mephitidae																
Conepatus leuconotus (Lichtenstein, 1832)	X				X			X								
Mephitis macroura Lichtenstein, 1832				X				X								
Mephitis mephitis (Schreber, 1776)				X				Λ								
				Λ	v			v				v				
Spilogale gracilis Merriam, 1890					X			X				X				
Family Procyonidae																
Bassariscus astutus (Lichtenstein, 1830)					X				X	X						
Nasua narica (Linnaeus, 1766)					X			X	X	X		X				
D 1 (11 4==0)				X	X			X	X	X		X				
Procyon lotor (Linnaeus, 1758)																
Procyon lotor (Linnaeus, 1758)  Order Artiodactyla  Family Tayassuidae																



 TABLE 2. Continued.

	VEGETATION TYPE CO													CO	I					
	UA	EA	XS	WD	SS	СН	EO	PO	TD	wo	TS	STS	CV	WA	CO					
Family Cervidae																				
Subfamily Cervinae																				
Odocoileus virginianus (Zimmermann, 1780)				X	X			X	X			X								
Order Rodentia																				
Family Sciuridae																				
Subfamily Sciurinae																				
Sciurus aberti Woodhouse, 1853								X							Pr					
Sciurus colliaei Richardson, 1839											X									
Sciurus nayaritensis J.A. Allen, 1890				X		X		X												
Otospermophilus variegatus (Erxleben, 1777)	X	X		X	X			X	X	X										
Tamias bulleri J.A. Allen, 1889		X		X		X		X							VU					
Tamias dorsalis Baird, 1855								X												
Tamias durangae (J.A. Allen, 1903)								X												
Xerospermophilus spilosoma (Bennett, 1833)		X																		
Family Heteromyidae																				
Subfamily Dipodomyinae																				
Dipodomys ornatus Merriam, 1894							X								Pr					
Subfamily Heteromyinae																				
Liomys irroratus (Gray, 1868)				X				X												
Liomys pictus (Thomas, 1893)		X							X	X	X	X	X	X						
Subfamily Perognathinae																				
Chaetodipus nelsoni (Merriam, 1894)	X	X		X	X				X											
Perognathus flavus Baird, 1855					X															
Family Geomyidae																				
Thomomys atrovarius (J.A. Allen, 1898)									X											
Thomomys sheldoni Bailey, 1915				X		X	X	X												
Thomomys umbrinus (Richardson, 1829)		X						X												
Family Cricetidae																				
Subfamily Arvicolinae																				
Microtus mexicanus (de Saussure, 1861)								X												
Subfamily Neotominae																				
Baiomys taylori (Thomas, 1887)		X		X	X			X			X		X	X						
Hodomys alleni (Merriam, 1892)												X								
Nelsonia neotomodon Merriam, 1897								X							Pr					
Neotoma leucodon Merriam, 1894		X	X	X			X													
Neotoma mexicana Baird, 1855			X	X		X		X	X			X		X						
Onychomys arenicola Mearns, 1896							X													
Peromyscus boylii (Baird, 1855)		X	X	X	X	X	X	X	X											
Peromyscus difficilis (J.A. Allen, 1891)				X		X		X												
Peromyscus eremicus (Baird, 1858)				X	X			X	X	X										
Peromyscus gratus Merriam, 1898		X		X		X	X	X		X										
Peromyscus leucopus (Rafinesque, 1818)		X		X					X											
Peromyscus maniculatus (Wagner, 1845)		X		X				X												
Peromyscus melanophrys (Coues, 1874)		X		X	X				X											
Peromyscus pectoralis Osgood, 1904		X	X	X	X			X	X	X										
Peromyscus schmidlyi Bradley et al., 2004				X		X	X	X												
Peromyscus simulus Osgood, 1904											X		X		VU					
Peromyscus spicilegus J.A. Allen, 1897								X	X	X	X	X		X						
Reithrodontomys fulvescens J.A. Allen, 1894		X		X	X				X	X	X									
Reithrodontomys zacatecae Merriam, 1901								X												
Subfamily Sigmodontinae																				
Oryzomys mexicanus J.A. Allen 1897											Х	X	Х	X	Α					
Sigmodon alleni Bailey, 1902										X	X	X			VU					
Sigmodon arizonae Mearns, 1890		X			X				X	X	X	X	X	X	. 0					
Sigmodon fulviventer J.A. Allen, 1889		X						X	**		**			**						
Sigmodon leucotis Bailey, 1902		<del>* •</del> ar		X				X												
				41				4.4		v		v								
										Х		Λ								
Sigmodon mascotensis J.A. Allen, 1897 Sigmodon ochrognathus Bailey, 1902				X						X		X								

 $<sup>^{\</sup>rm 1}\,\mbox{Species}$  probably extirpated from the area.



the tropical elements that penetrate into the basin as far as Candelaria del Alto, Durango (site 3 on Figure 1). Similarly, species like the nectar-feeding bat Anoura geoffroyi Gray, 1838 or the fruit bat *Dermanura azteca* are able to reach the highlands of the central portion of the SMO, at elevations of 2600 m in pine-oak forest. Another tropical species, Sigmodon arizonae, occurs throughout the river valley, as far north as the vicinity of Vicente Guerrero, Durango, at the western edge of the Mexican Plateau. Conversely, species of Nearctic affinities like the bat *Myotis* yumanensis, a common inhabitant of the Chihuahuan Desert, Mexican Plateau and mountainous areas, reach as far south into the basin as San Blasito Nayarit (site 6, Figure 1), on the western slope of the Sierra, in an area where tropical deciduous and semideciduous forest dominate. Thus, group 3 in Figure 3 includes those plant communities that co-occur and intermingle in the river canyon. Each contains more species than otherwise would be expected because they share them with neighboring vegetation associations.

Results of recent studies on vascular plants have suggested that the river valley is a potentially continuous corridor between arid and semiarid regions from the Mexican Plateau, and tropical deciduous forest from the western slope of the Sierra (González-Elizondo *et al.* 2007). For most mammalian species this seems to be the case, although for many it is only a partial corridor, *i.e.*, Neotropical species stay associated to Neotropical elements as far as they reach into the basin, but not beyond.

SPMRB compared to other areas.---Species richness in the basin was considerably higher than that of Mexico for Chiroptera and Carnivora, but considerably smaller for Rodentia (Figure 2). Although it is possible that these numbers represent the true proportions at the basin, it is more likely that the underrepresentation of rodents is due to collection bias. Because rodents may have distributions that are restricted to small areas and microhabitats, and because sampling is far from complete, we may be missing species with restricted distributions. Evidence that this is more than speculation is the description of a new species of deer mouse Peromyscus carletoni Bradley et al., 2014, or the pocket gopher Thomomys nayarensis Mathis et al., 2013b from the highlands of Nayarit, in areas very close to SPMRB, and associated to vegetation types that also are present in the basin. The apparent overrepresentation of bats and carnivores might just be the result of the relatively low numbers of recorded rodents, which lowers the percentage of the latter while increasing that of the former.

Because of its geographic position at the Nearctic–Neotropical transition, we expected to find a high species richness in the basin (Ortega and Arita 1998; Morrone 2005). Moreover, richness would be expected to be similar to that of other Nearctic–Neotropical transitional areas. Species richness in the basin was higher than in any other Nearctic–Neotropical transition documented, and it is as high as the most diverse Neotropical areas in Mexico, except for Los Tuxtlas (Figure 7). This can be explained because in other Nearctic–Neotropical gradients change occurs from tropical to temperate vegetations, whereas at SPMRB the Nearctic–Neotropical transition includes not only tropical lowland vegetations to highland, temperate pine and pine-

oak vegetation (on the western flank), but also, a transition from lowland tropics or pine-oak vegetation to semi-arid vegetations typical of the Mexican Plateau on the eastern slope of the Sierra. Another well documented region where a similar transition occurs is the Tehuacán-Cuicatlán valley in south-central Mexico (González-Ruíz *in litt.;* SEMARNAT 2013), which nonetheless had considerably lower species richness. Manantlán, on the other hand, is at the transition between the neotropics and the Mexican Transvolcanic Belt, an area in itself very diverse (Fa and Morales 1991; Íñiguez-Dávalos and Santana-Castellón 2005), which accounts for its high richness, similar to that of SPMRB.

Proportion of endemic species is also high at the SPMRB compared with other areas of Mexico. Neotropical sites are very species-rich, but most species are shared with the tropical biomes of Central and South America and therefore there is low endemism (Ceballos *et al.* 1998). Along the Sierra Madre Oriental, most species of Nearctic affinities are shared with the USA, and most species of Neotropical affinities are shared with the Neotropics, therefore endemism levels are low except in its southern portion. The highest levels of endemism in Mexico are along the western mountain ranges (SMO, Sierra Madre del Sur) and the Transvolcanic Belt, areas of rugged topography and biogeographic transition (Ceballos *et al.* 1998; Ceballos and Martínez 2010).

## Conclusions and remarks

Our results indicate that the SPMRB is one of the most species-rich areas of Mexico. Species numbers are comparable to those of highly diverse tropical areas and higher than most Nearctic-Neotropical transitions documented so far for Mexico, and the species number will continue to increase as survey and inventory efforts continue (e.g., Tapia-Ramírez et al. 2013). SPMRB also harbors a large number of endemic species, which very likely also will rise as microhabitats are discovered and sampled. The topographic complexity that produces a large number of unique combinations of climates and vegetation, and therefore of potential microhabitats, very likely drives active processes of diversification in some areas of the basin, particularly on the central and southern portions. Therefore, species richness, in particular of rodents and shrews, probably is greater than currently reported.

Geographic areas with high species richness and rare, endemic, or threatened species historically have been the focus of conservation efforts (Mittermeier *et al.* 1998; Reid 1998). At SPMRB 20% of species are endemic of Mexico, and 15.1% are under some status of concern. Also, the basin is an area of high local diversity ( $\alpha$ -diversity), high species turnover rate at short distances ( $\beta$ -diversity), and therefore of high regional megadiversity ( $\gamma$ -diversity) (Arita and Rodriguez 2002; Rodríguez *et al.* 2003).

Conservation efforts should focus not only on the biodiversity value of the areas to be preserved, but also on the ecosystem services they are able to provide (Turner *et al.* 2007), and on their cultural value ("cultural services", see Daniel *et al.* 2012). Zones of high biological diversity often are linguistically and therefore culturally diverse as well (Gorenflo *et al.* 2012). At SPMRB, five human cultures (mestizo, tepehuano, mexicanero, huichol and cora) and

as many languages coexist and interact. Additionally, the San Pedro-Mezquital River is so far the only one that remains undammed on the Pacific versant (although a hydroelectric project is ongoing, Gobierno del Estado de Nayarit 2010), and it is the main source of water for all human activities within the basin (WWF 2010), including domestic use (mainly Durango city on the eastern versant), as well as agricultural (on the Guadiana Valley in Durango and the Pacific plain of Nayarit) and cattle ranching activities (throughout the basin). Also, it is one of the main water sources for the Marismas Nacionales, one of the largest wetland ecosystems of the Mexican Pacific (CONANP 2007). Thus, it is not surprising that in a recent assessment, the SPMRB laid in an area of high biodiversity value and ecosystem services value (Turner *et al.* 2007).

The scenario of complexity and the relative inaccessibility of the central area of the basin preclude the development of large human settlements and the establishment of the large scale agricultural modification that characterizes the coastal plain or the Mexican Plateau. Therefore, at least part of the basin is a good candidate for a protection and management area. One already protected area (La Michilía biosphere reserve) and three conservation priority areas lie within the basin (Guacamayita, Marismas Nacionales, and La Michilía, Arriaga *et al.* 2000). We urge peoples and government instances of the area to open the discussion as to how better manage and preserve one of the most diverse areas of Mexico.

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**APPENDIX 1. Voucher specimens.** Species and catalog number of one specimen collected by us, and total number of specimens collected (in parenthesis) is given for each species. If no specimen was available from our collections (CRD), catalog number of a specimen from another collection examined by us is given.

Didelphis virginiana: CRD-475 (6). Tlacuatzin canescens: CRD-6430 (2). Dasypus novemcinctus: JFCM-462 (3). Lepus californicus: CRD-7076 (3). L. callotis: CRD-331 (3). Sylvilagus audubonii: CRD-724 (3). S. cunicularius: KU--85729. S. floridanus: CRD-7078 (6). Notiosorex crawfordi: CRD-786 (1). Sorex emarginatus: ENCB-14233. Balantiopteryx plicata: CRD-7085 (48). Desmodus rotundus: CRD-4685 (13). Anoura geoffroyi: CRD-4686 (13). Choeronycteris mexicana: CRD-4688 (18). Glossophaga commissarisi: CRD-7517 (2). G. leachii: CRD-7260 (14). G. soricina: CRD-4691 (75). Leptonycteris nivalis: CRD-4711 (1). Le. yerbabuenae: CRD-4697 (57). Glyphonycteris sylvestris: CRD-7237 (12). Macrotus californicus: CRD-4681 (36). Artibeus hirsutus: CRD-4712 (100). A. intermedius: CRD-4741 (34). A. jamaicensis: CRD-7319 (69). Centurio senex: CRD-7374 (10). Chiroderma salvini: CRD-6458 (3). Dermanura azteca: CRD-4751 (9). D. phaeotis: CRD-7384 (6). D. tolteca: CRD-7390 (68). Sturnira parvidens: CRD-4759 (46). Mormoops megalophylla: CRD-7136 (38). Pteronotus davyi: CRD-7175 (17). P. parnellii: CRD-6431 (32). P. personatus: CRD-6175 (18). Noctilio leporinus: CRD-6174 (4). Natalus mexicanus: CRD-7396 (25). Molossus rufus: CRD-7424 (2). Nyctinomops femorosaccus: CRD-4844 (8). N. macrotis: CRD-4849 (5). Tadarida brasiliensis: CRD-4854 (43). Eptesicus fuscus: CRD-4833 (33). Lasiurus blossevillii: CRD-271 (10). La. cinereus: CRD-3 (7). La. xanthinus: CRD-215 (2). Rhogeessa parvula: CRD-7421 (6). Parastrellus hesperus: CRD-4838 (49). Corynorhinus mexicanus: CRD-4830 (1). C. townsendii: CRD-8111 (4). Euderma maculatum: ENCB-14252. Idionycteris phyllotis: CRD-8135 (1). Antrozous pallidus: CRD-455 (20). Myotis auriculus: ENCB-10292. M. californicus: CRD-4770 (30). M. carteri: CRD-7420 (1). M. melanorhinus: CRD-6248 (9). M. thysanodes: CRD-4776 (6). M. velifer: CRD-4778 (118). M. volans: CRD-1543 (2). M. yumanensis: CRD-4772 (62). Leopardus wiedii: CRD-7425 (1). Lynx rufus: CRD-4861 (2). Puma concolor: CRD-7651 (1). Panthera onca: CRD-6606 (1). Canis latrans: ENCB-10631. C. lupus: MSU-23667. Urocyon cinereoargenteus: CRD-193 (5). Ursus americanus: MSU-871. Lontra longicaudis: CNMA-38266. Conepatus leuconotus: CRD-476 (2). Mephitis macroura: CRD-195 (3). Me. mephitis: CRD-936 (1). Spilogale gracilis: CRD-8211 (1). Bassariscus astutus: CRD-6763 (1). Nasua narica: CRD-7652 (3). Procyon lotor: CRD-5134 (5). Pecari tajacu: CRD-6764 (1). Odocoileus virginianus: CRD-5136 (7). Sciurus aberti: MSU-3334. Sc. colliaei: KU-85732. Sc. nayaritensis: CRD-1546 (1). Otospermophilus variegatus: CRD-106 (9). Tamias bulleri: CRD-1547 (7). T. dorsalis: ENCB-14253. T. durangae: MSU-3331. Xerospermophilus spilosoma: BYU-22232. Dipodomys ornatus: MSU-1097. Liomys irroratus: CRD-109 (5). Li. pictus: CRD-

6180 (139). Chaetodipus nelsoni: CRD-110 (340). Perognathus flavus: CRD-6952 (7). Thomomys atrovarius: MSU-16504. Th. sheldoni: CRD-15 (2). Th. umbrinus: CRD-368 (2). Microtus mexicanus: ENCB-523. Baiomys taylori: CRD-1532 (38). Hodomys alleni: CRD-7720 (2). Nelsonia neotomodon: ENCB-10605. Neotoma leucodon: CRD-178 (5). Ne. mexicana: CRD-1003 (29). Onychomys arenicola: MSU-1459. Peromyscus boylii: CRD-1527 (38). Pe. difficilis: CRD-1000 (67). Pe. eremicus: CRD-167 (155). Pe. gratus: CRD-1553 (13). Pe. leucopus: CRD-173 (7). Pe. maniculatus: CRD-123 (29). Pe. melanophrys: CRD-5491 (15). Pe. pectoralis: CRD-170 (197). Pe. schmidlyi: CRD-1006 (48). Pe. simulus: CRD-7477 (10). Pe. spicilegus: CRD-7729 (117). Reithrodontomys fulvescens: CRD-113 (38). R. zacatecae: CRD-19 (2). Oryzomys mexicanus: CRD-7475 (4). Sigmodon alleni: CRD-7491 (3). Si. arizonae: CRD-6617 (26). Si. fulviventer: CRD-1537 (9). Si. leucotis: CRD-1009 (7). Si. mascotensis: CRD-6610 (91). Si. ochrognathus: CRD-176 (2).